Reference: *Biol. Bull.* **151**: 560–573. (December, 1976)

DEVELOPMENT AND METAMORPHOSIS OF THE SEA-STAR, *ASTROPECTEN SCOPARIUS* VALENCIENNES

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The development of sea-stars has been reported in a number of species (reviewed by MacBride, 1914; Hyman, 1955; Dan, 1957; Hayashi, 1972). However, it seems that enough information has not been available on the entire process of the development and the metamorphosis to make it possible to discuss the phylogenetic significance of developmental features, as well as of the post-metamorphic growth.

The development of sea-stars is generally divided into two types, the indirect and the direct. In the former, the embryo develops into brachiolaria after passing through bipinnaria as reported in *Asterias rubens, Asterias amurensis* and *Acanthaster planci* (Gemmill, 1914; Dan, 1957; Henderson and Lucas, 1971). In the direct development, only brachiolaria appears, and the bipinnaria stage is entirely lacking. This type of development has been reported in a number of species as exemplified by *Asterina gibbosa, Henricia sanguinolenta, Certonardoa semiregularis* and *Echinaster echinophorus* (MacBride, 1896; Masterman, 1902; Hayashi and Komatsu, 1971; Atwood, 1973). However, development of the species belonging to the genus *Astropecten* may not be exactly classified into either of the two types mentioned above, since they undergo metamorphosis while larvae are pelagic, usually as a bipinnaria, and lack the brachiolaria stage completely. The development of *Astropecten aranciacus* may illustrate a typical process of abrachiolarian type of development (Hörstadius, 1939). Mortensen (1921, 1937) gave brief notes on metamorphosing larvae of two Japanese astropectens, *Astropecten scoparius* and *Astropecten polyacanthus* and showed that the metamorphosis of these species may occur without passing through brachiolaria stage. Furthermore, brief accounts were recently presented on the early development of these two astropectens (Komatsu, 1973; Oguro, Komatsu and Kano, 1975). However, the details of the entire process of the development of these two species remain unknown.

Since there is a noticeable feature in the development of *Astropecten* species as noted above, it is important to learn the development of this group in detail, especially its metamorphosis, for a thorough understanding of the significance of development in sea-stars.

The writers have had opportunities to observe the development of *Astropecten scoparius* in the last few years, and the following is a description of the entire process of its development in terms of external morphology and skeletal system formation.

Materials and Methods

Adults of *Astropecten scoparius* Valenciennes were collected along the coast of Toyama Bay, Sea of Japan. The present species is one of the most common

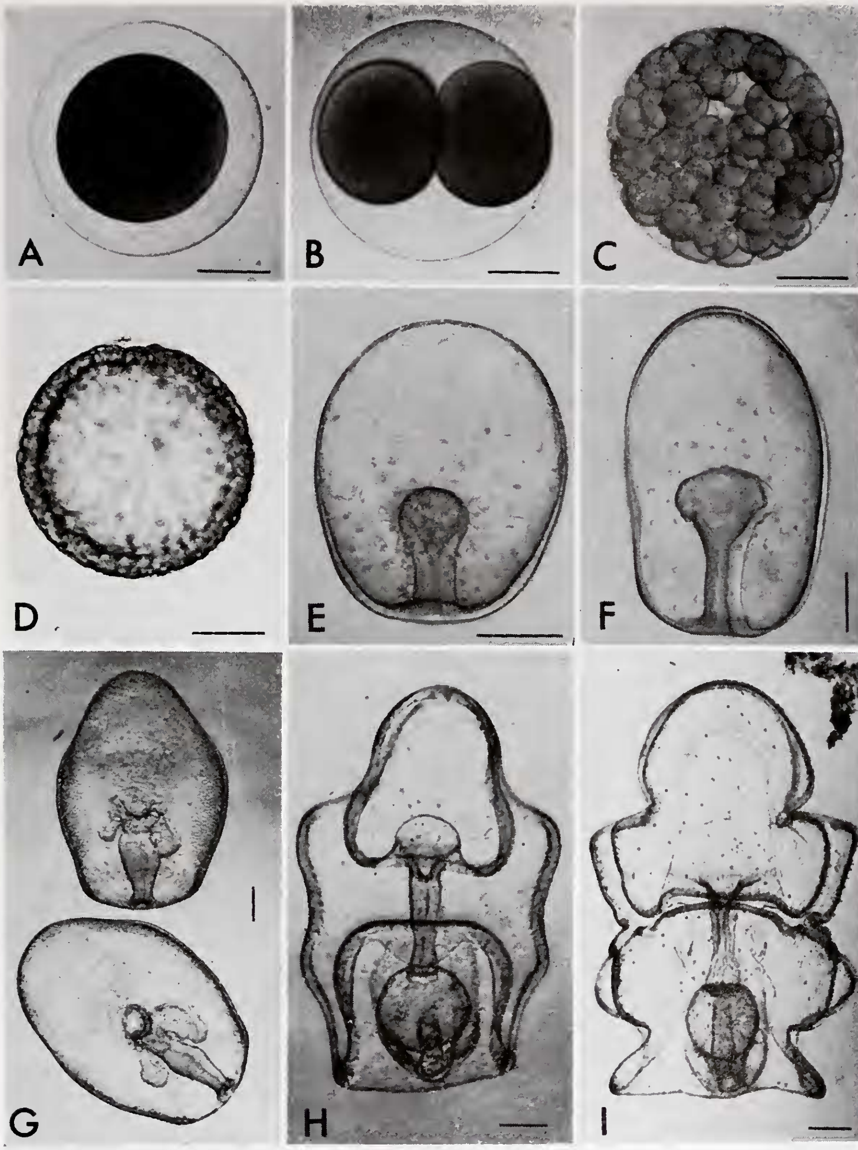


FIGURE 1. Development of *Astropecten scoparius.* All pictures show living specimens; scale = 100 μ: A) fertilized egg with complete fertilization membrane; B) two-cell stage; C) early blastula; D) coeloblastula; E) gastrula, 15 hours after insemination; F) gastrula, 20 hours after insemination; G) early bipinnaria, 35 hours after insemination, ventral view; H) bipinnaria, 48 hours after insemination, ventral view; and I) bipinnaria, 80 hours after insemination, ventral view.

sea-stars in Japan. This species is gonochristic. The gonad, in both sexes, is composed of tufted tubules and restricted to the base of each arm. Each gonad is furnished with a gonoduct which opens on the aboral side of the arm base. The breeding season in Toyama Bay is estimated to be July–August.

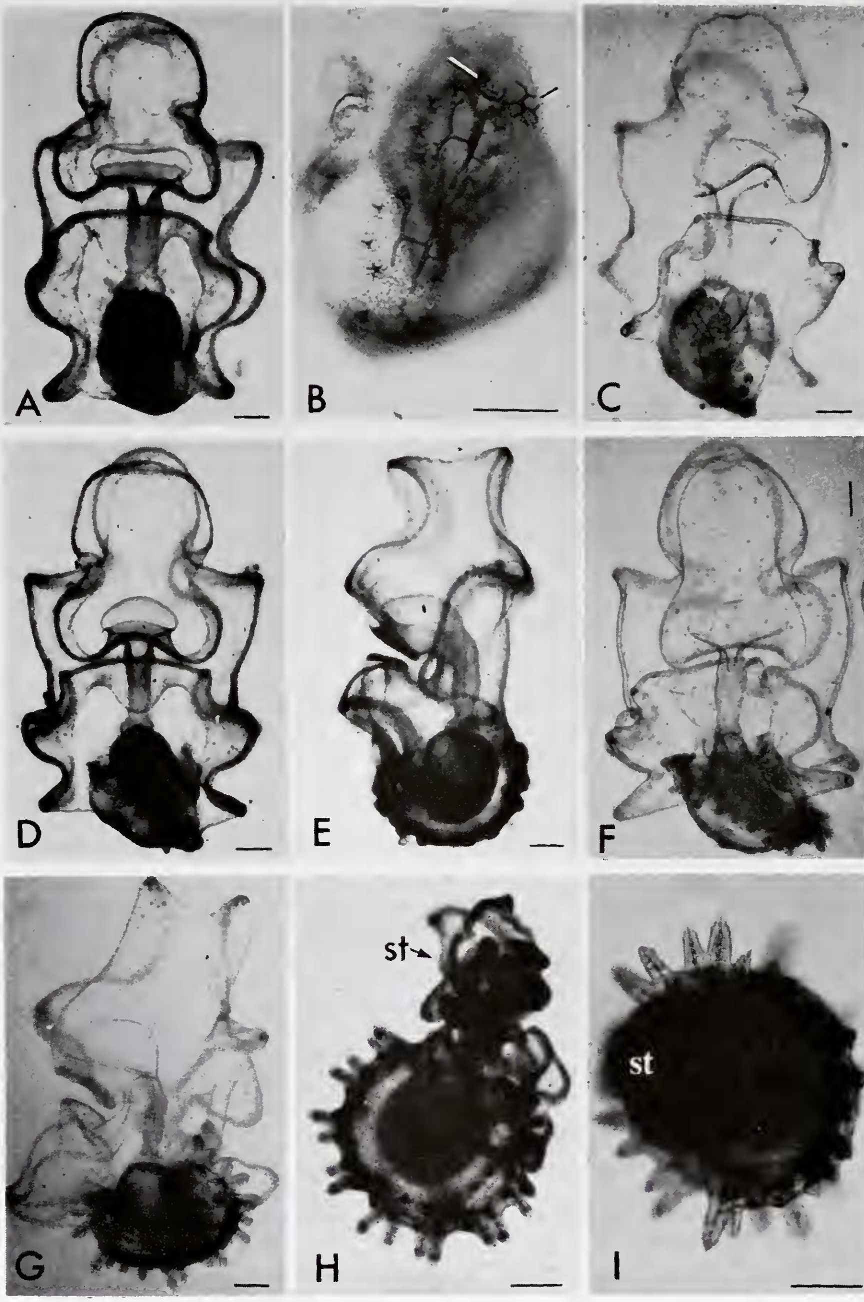


FIGURE 2. Development of *Astropecten scoparius.* All pictures show living specimens; scale = 100 μ: A) bipinnaria, 7 days after insemination and at the onset of metamorphosis, ventral view; B) enlarged picture of the posterior portion of the metamorphosing bipinnaria, the same specimen as shown in Figure 4B—short and long arrows point to rudimental

Observations were mostly made on materials obtained by artificial fertilization as will be described below. Ovaries were dissected out and placed in petri-dishes, in which a seawater solution of 1-methyladenine was applied to induce the completion of maturation and spawning (see Kanatani, 1969). Twenty to 60 minutes thereafter, mature ova were released from the ovaries. The spawned ova were removed and washed thoroughly. A few drops of sperm suspension were applied to the dishes containing the mature ova. In addition to the artificially raised embryos, observations on the later development were supplemented by materials from natural spawning in aquaria of Uozu Aquarium, and from collection in the field. Standard temperature for the development in the laboratory was 25° C. For the observations of external morphology, specimens were studied by light microscope or phase-contrast microscope. Examinations of the skeletal system were mostly performed after treatment with KOH solution. In addition, skeletal plates of the juveniles were observed by scanning electron microscope after the treatment by KOH and sonication. Sea water used in the standard observations in the laboratory was obtained from the coast of Toyama Bay and filtered before use. Average salinity was 34‰ and pH was 8.3.

Observations and Results

The mature ova are spherical, translucent, approximately 230 μ in diameter, and are enclosed in a jelly layer about 1 μ thick. They are heavier than sea water. About 5 minutes after insemination, the fertilization membrane began to elevate, and 40 minutes thereafter the process was completed with a perivitelline space 50 μ in height (Fig. 1A). One hour after insemination, the first cleavage occurred through the animal-vegetal axis (Fig. 1B). The embryos were in the 4-cell stage 100 minutes after insemination, and in the 32-cell stage 150 minutes after insemination. The cleavage is of the holoblastic radial type (Fig. 1C), and they developed into coeloblastulae 5 hours after insemination (Fig. 1D). Then, the wrinkled blastula stage began and it continued for about 4 hours. The details of the wrinkled blastula stage of the present species have been described previously (Komatsu, 1973). Nine and a half hours after insemination, gastrulation by invagination took place from the vegetal pole. Ten hours after insemination, early gastrulae began to rotate within the fertilization membrane, and they hatched 40 minutes thereafter. Gastrulae just after hatching were 250 μ in length. They gradually elongated along the archenteric axis, and 15 hours after insemination they measured 350 μ in length and 270 μ in width (Fig. 1E). The blind end of the archenteron expanded, showing the differentiation of the future coelomic pouches. Mesenchymal cells were set free into the blastocoel. Five to

madreporic plate and hydropore, respectively; C) metamorphosing bipinnaria, slightly later than that shown in Figure 4B, ventro-lateral (right) view; D) metamorphosing bipinnaria, 10 days after insemination, the same stage as shown in Figure 4D, E and F, (ventral view); E) lateral (left) view of the same specimen shown in Figure 2D; F) metamorphosing bipinnaria, 12–13 days after insemination, ventral view; G) lateral view (left) of the same specimen shown in Figure 2F; H) metamorphosing bipinnaria with shrunken stalk (st), future aboral side view; and I) metamorphosing juvenile with rudimental larval stalk (st), future oral side view.

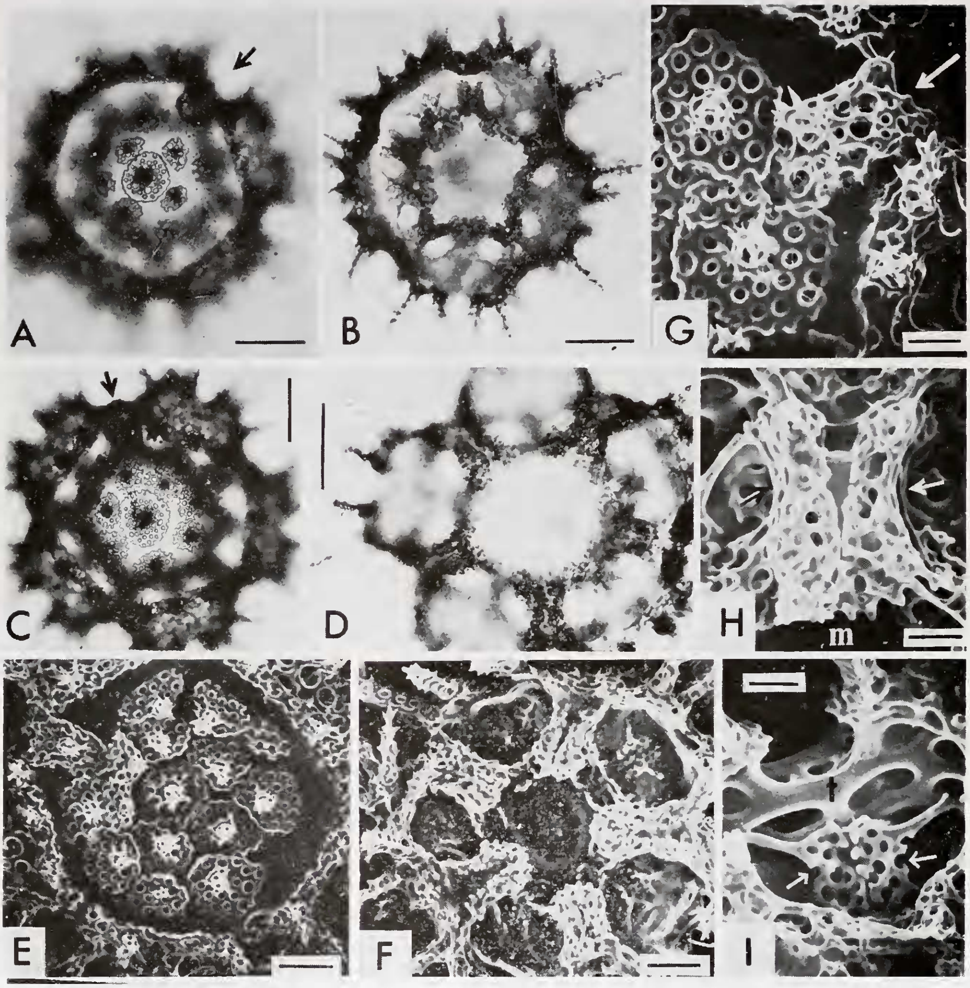


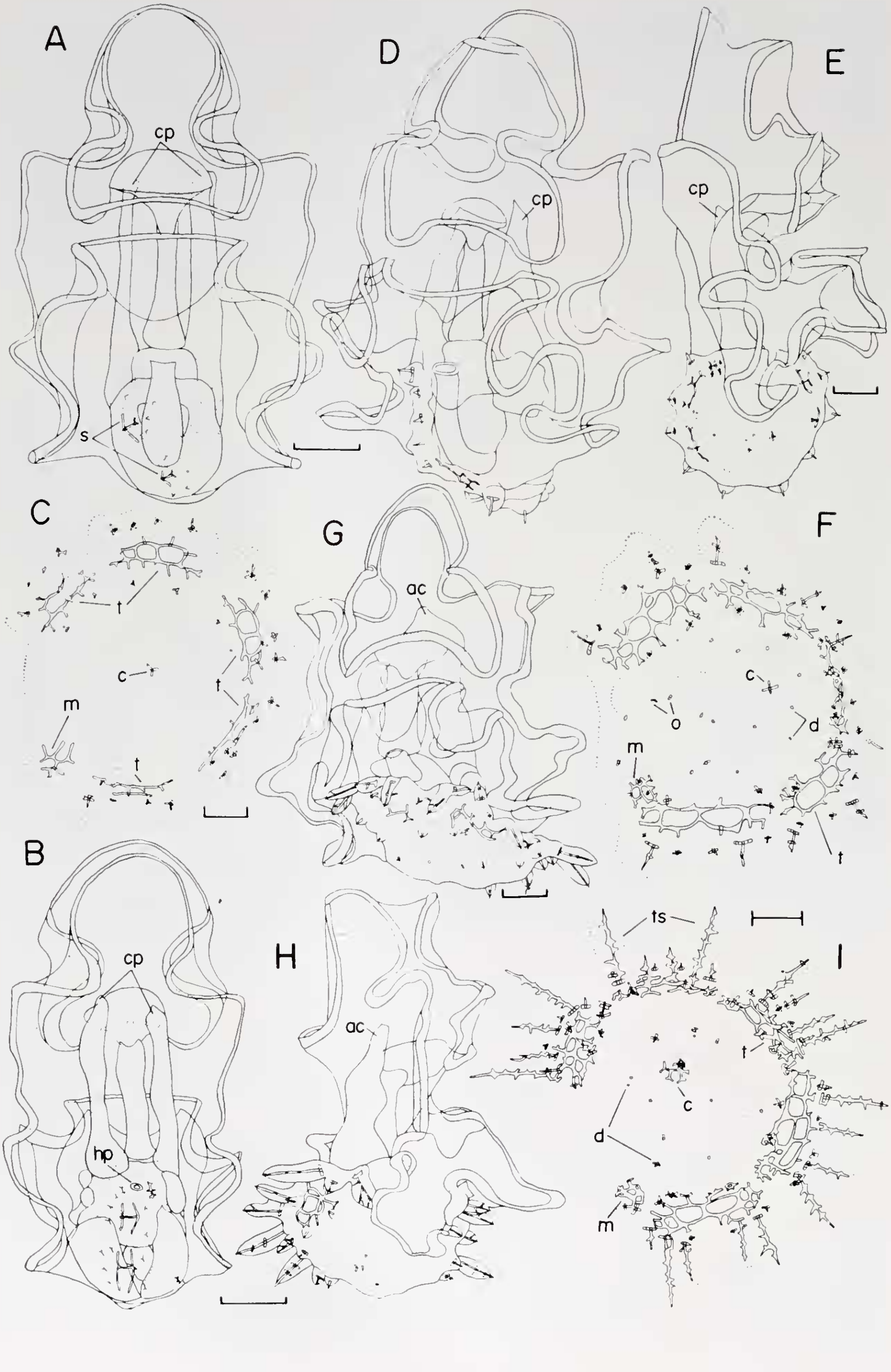
FIGURE 3. Development of *Astropecten scoparius*. All specimens were preserved and treated with KOH solution. Scale = 100 μ in A–D: A) aboral skeletal plates of a juvenile, 18 days after insemination and immediately after metamorphosis—arrow (upper right) shows madreporic plate; B) oral skeletal plates of the same specimen shown in Figure 3A; C) aboral skeletal plates of a juvenile, 23 days after insemination—arrow shows madreporic plate; and D) oral skeletal plates of the same specimen shown in Figure 3C. Figure 3 E–I, shows scanning electron microscopy. Scale = 50 μ in E and F; 25 μ in G–I: E) aboral skeletal plates of a juvenile, one month after insemination; F) oral skeletal plates of the same specimen shown in Figure 3E; G) madreporic plate (arrow) of a juvenile, 1 month after insemination; H) a pair of oral plates (arrows) of a juvenile, one month after insemination (m shows mouth); and I) a pair of ambulacral plates (arrows) of a juvenile, one month after insemination (t, terminal plate).

7 hours thereafter, a pair of the rudimental coelomic pouches was distinguishable at both sides of the top of the archenteron (Fig. 1F). The length and the width of this specimen were 600 μ and 450 μ, respectively. At this time, the oral depression was recognized on the future ventral side of the larva. Thirty-five hours

after insemination, 2 ciliary bands became obvious and the larva could be called a bipinnaria. The archenteron began to differentiate into intestine, stomach and esophagus which opens at the oral depression. The hydropore opened in the left coelomic pouch, which is at this time larger than the right one (Fig. 1G). Forty-eight hours after insemination, the length and the width of the bipinnaria were 850 μ and 600 μ, respectively. The left and the right coelomic pouches were separated from the digestive tract, and each coelomic pouch was constricted at the middle portion into two parts, the anterior (hydrocoel) and the posterior (stomatocoel) (Fig. 1H). Eighty hours after insemination, the bipinnaria grew to a considerable size, 1,000 μ in length and 650 μ in width, and the ventral horn was well-developed between the intestine and the stomach (Fig. 1I).

About one week after insemination, the posterior portions of the bipinnariae, which were reared in the aquaria, became swollen and the gastric portion became rather opaque (Fig. 2A). Shortly thereafter, several spicules were formed on the posterior portion of the bipinnariae (Fig. 4A). These spicules were not larval ones, but they were the rudiments of the future terminal plates of the juveniles. Average length of the bipinnariae of this stage was 1,150 μ, although remarkable variation exists in the progress of the development and in the size of the larvae in the present species. The larvae of the present material were far larger than those reported by Mortensen (1937) as a fully grown bipinnaria (600 μ in length) of this species. Primordia of 5 hydrolobes then appeared in the posterior end of the left hydrocoel. Metamorphosing bipinnaria shown in Figure 4B was one day after that shown in Figure 4A. Enlarged pictures of the spicules of this specimen are shown in Figure 2B. Thereafter, the posterior part of the larvae was transformed progressively into a subpentagonal sea-star shape, while the anterior part was kept almost unchanged for a few days (Fig. 2C). The aboral skeletal system at this stage was composed of one central plate and one madreporic plate, in addition to five terminal plates, each furnished with several spines (Fig. 4C). About ten days after insemination, the disk of the future juvenile sea-star was well marked from the bipinnaria stalk and the aboral portion of the future disk could be observed from the right side of the larva (Figs. 2D, 2E, 4D, 4E). In this stage, the rudiments of five pairs of oral plates and those of several dorsal plates around the central plate were formed on the future oral and aboral side, respectively (Fig. 4F). Two days thereafter, the hydrocoelomic pouches in both sides extended so as to contact each other at the anterior ends (Figs. 4G, 4H). At this time, two spines on the edge of the terminal plates became extremely long (Fig. 4I). Five pairs of the rudimental ambulacral plates were set on the future oral side of the juveniles (Fig. 5A). About 12–13 days after insemination, the anterior part of the larva still kept the typical form of the bipinnaria of this species (Figs. 2F, 2G).

About two weeks after insemination, the stalk, the anterior portion of the bipinnaria, began to shrink rapidly, and thus the progress of the metamorphosis seemed to be accelerated at this time (Fig. 2H). On the other hand, Mortensen (1921) reported that the metamorphosis of the present species is initiated three weeks after insemination. The metamorphosing bipinnariae with shrunken stalk sank to the bottom; then the ciliary bands became inconspicuous due to the extreme reduction of the stalk (Figs. 5B, 5C). The reduced stalk disappeared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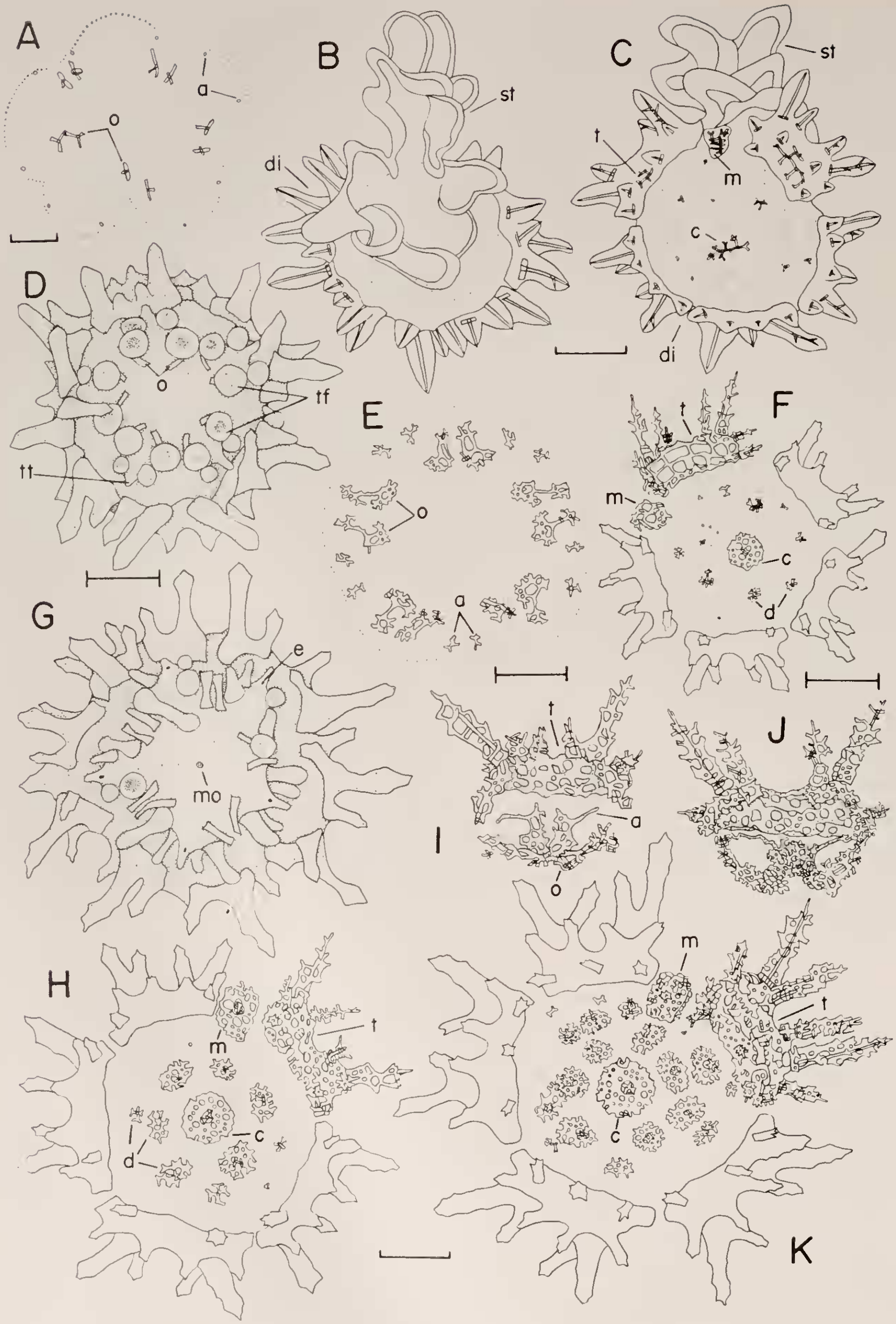
within a few days (Fig. 2I). Then the primordia of two pairs of tube-feet and of a single terminal tentacle appeared on each hydrolobe. About 16 days after insemination, the metamorphosing juveniles could move slowly on the substratum by means of their tube-feet (Fig. 5D). It is worth notice that the tube-feet of these juveniles are suckered, while the tube-feet of the adult lack suckers. Examination of the serial sections of these juveniles showed that they lack anus as in the adults. The diameter of these juveniles was about 500 μ including marginal spines. The skeletal system of this stage is shown in Figures 5E and 5F.

About 18 days after insemination, the mouth opened and thus metamorphosis was completed (Fig. 5G). Juveniles immediately after metamorphosis were white in color with a pale brown portion at the center of the disk and about 600 μ in diameter. Each arm bore two pairs of the tube-feet and a terminal tentacle with an eye-spot of red color. On the aboral side of the disk, about 10 plates were recognized in addition to one central plate and one madreporic plate (Figs. 3A, 5H.) However, radial plates were not distinguishable from the interradial plates because of their irregular arrangement. Figures 3B and 5I represent the skeletal system of the oral side of the juvenile just after metamorphosis. The features of the skeletal system of newly metamorphosed juveniles of the present species are very similar to those of *Astropecten aranciacus* and *Astropecten latespinosus* (Hörstadius, 1939; Komatsu, 1975a). About five days after the completion of metamorphosis, juveniles grew to about 700 μ in diameter. During these days, skeletal formation progresses further (Figs. 3C, D; 5J, K). Scanning electron microscopy illustrates the stereo-structure of the skeletal system of juveniles one month after the completion of metamorphosis (Fig. 3E–I).

After the completion of laboratory observations, a field survey of the juveniles was carried out by SCUBA diving in the area where the adults inhabit. The following descriptions are based on these collections. The smallest specimens collected in October and November were 2.2 and 1.7 mm in R (the distance from the center of the disk to the arm tip), respectively. Since the breeding season of the present species in Toyama Bay is presumed to be July–August as noted before, the juveniles grew from 600 μ to 3.5–4.0 mm in diameter during these two to three months.

FIGURE 4. A) Metamorphosing bipinnaria, 7 days after insemination, ventral view; cp, coelomic pouch; s, spine; scale = 150 μ. B) Metamorphosing bipinnaria, one day after that shown in Figure 4A, dorsal view: cp, coelomic pouch; hp, hydropore; scale = 150 μ. C) Skeletal system of metamorphosing bipinnaria, the same stage as shown in Figure 2C, view from the future aboral side of the juvenile: c, central plate; m, madreporic plate; t, terminal plates; scale = 50 μ. D) Metamorphosing bipinnaria, 10 days after insemination, the same stage as shown in Figure 2D and E: cp, coelomic pouch; scale = 150 μ. E) Lateral (right) view of the same specimen shown in Figure 4D: cp, coelomic pouch; scale = 100 μ. F) Skeletal system of metamorphosing bipinnaria, the same stage as shown in Figure 4D and E, view from the future aboral side of the juvenile: c, central plate; d, dorsal plates; m, madreporic plate; o, oral plates; t, terminal plate; scale = 50 μ. G) Metamorphosing bipinnaria, 12 days after insemination, ventral view; ac, anterior coelom; scale = 100 μ. H) Lateral (right) view of the specimen shown in Figure 4G: ac, anterior coelom; scale = 150 μ. I) Skeletal system of the dorsal side of metamorphosing bipinnaria, the same stage as shown in Figure 4G and H, view from the future aboral side of the juvenile: c, central plate; d, dorsal plates; m, madreporic plate; t, terminal plate; ts, spines of the terminal plates; scale = 50 μ.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Although it has been well known that some diagnostic features are not developed in small-sized specimens of sea-stars, no substantial studies have been previously carried out. In the present study, the development of some diagnostic features was observed on the post-metamorphosed specimens. In the adults, superomarginal plates are each furnished with one long spine excepting the interbrachial arch, and this is designated as one of the diagnostic features of the present species. However, no spines are found in the superomarginal plates in specimens smaller than 9.0 mm in R or having less than 30 pairs of tube-feet in one arm. Studies were then extended to the R/r value (a ratio between R, the distance from the center of the disk to the arm tip, and r, the distance from the center of the disk to the middle of the interbranchial margin). The R/r value is used as a general mark in the description of asteroids, and 3–4 is noted in the present species. Examination of the present material showed that specimens smaller than 9 mm in R show less than 3.0 or even less than 2.0. A R/r value showing more than 3 is found in specimens larger than 9 mm in R. Observations were also made on the paxillae. Paxillae of specimens ranging from 4 to 9 mm in R are furnished with 5–6 peripheral spines but lack central spines. Central spines are formed in specimens larger than 9 mm in R. Then paxillar spines increase in number as the juveniles grow. In a specimen reaching 14.6 mm in R, the majority of the paxillae are furnished with 4 central and 12 peripheral spines. Since in fully grown adults, the largest paxillae are furnished with 10–15 central and 15–18 peripheral spines (Hayashi, 1973), formation of paxillae is completed more than two months after metamorphosis. These facts show that in *Astropecten scoparius* specimens smaller than about one cm in R bear poor diagnostic features.

Discussion

The early development of astropectens in all six species so far reported is very similar in the following points: total equal cleavage, coeloblastula, and wrinkled blastula formation (Metschnikoff, 1885; Mortensen, 1921, 1937; Newth, 1925;

FIGURE 5. A) Skeletal system of metamorphosing bipinnaria, the same stage as shown in Figure 4G, H and I, view from the future oral side of the juvenile. Dotted line shows an outline of 5 hydrolobes: a, ambulacral plates; o, oral plates; scale = 40 μ. B) Metamorphosing bipinnaria with shrunken stalk, little later than that shown in Figure 2H, view from the future oral side: di, disk; st, stalk; scale = 100 μ. C) Opposite of the specimen shown in Figure 5B: c, central plate; di, disk; m, madreporic plate; st, stalk; t, terminal plate; scale = 100 μ. D) Metamorphosing juvenile, 16 days after insemination, view from the future oral side: o, oral plates; tf, tube-feet; tt, terminal tentacle; scale = 100 μ. E) Skeletal system of the oral side of the specimen shown in Figure 5D: a, ambulacral plates; o, oral plates; scale = 50 μ. F) Skeletal system of the aboral side of the specimen shown in Figures 5D and E: c, central plate; d, dorsal plates; m, madreporic plates; t, terminal plate; scale = 100 μ. G) Oral side of a juvenile immediately after the completion of metamorphosis, 18 days after insemination: e, eye-spot; mo, mouth; scale = 100 μ. H) Skeletal system of the juvenile shown in Figures 3A, B and 5G, aboral view: c, central plate; d, dorsal plates; m, madreporic plate; t, terminal plate; scale = 100 μ. I) Skeletal system of a ray of a juvenile shown in Figure 5G, oral view: a, ambulacral plate; o, oral plate; t, terminal plate; scale = 50 μ. J) Skeletal system of a ray of a juvenile, 5 days after the completion of metamorphosis, the same stage as shown in Figure 3D, oral view; scale = 100 μ. K) Skeletal system of the aboral side of a juvenile, 5 days after the completion of metamorphosis: c, central plate; m, madreporic plate; t, terminal plate; scale = 100 μ.

Hörstadius, 1939; Komatsu, 1973, 1975a; Oguro *et al.*, 1975). In the present study, it was found that the entire process of the development of *Astropecten scoparius* resembles that reported in *Astropecten aranciacus* (Hörstandius, 1939). They undergo metamorphosis while larvae are pelagic as bipinnaria, although there are some minor differences between them. Among those, the difference in the term of larval life seems to be noticeable. Although various factors such as temperature, food or population density could considerably affect the progress of development, a conspicuous difference found between the two species is unlikely due to an environmental cause (18 days in the present species versus 90 days in *Astropecten aranciacus* to complete metamorphosis). In *Astropecten aranciacus*, fully grown bipinnariae are furnished with well-developed bipinnaria arms and highly complex ciliary bands (Hörstadius, 1939; Figs. 22 and 23). On the other hand, the bipinnaria of the present species just before metamorphosis is fairly simple. The bipinnaria of *Astropecten scoparius* thus initiates metamorphosis prematurely in comparison to *Astropecten aranciacus*, with regard to the form of the bipinnaria. This may relate to the nutritional condition of the species. Eggs of *Astropecten scoparius* are larger and more lecithotropic than those of *Astropecten aranciacus*, in which a much longer term is needed to prepare for initiating metamorphosis. In this context, the development of *Astropecten latespinosus* is of special interest (Komatsu, 1975a). The eggs of *Astropecten latespinosus* is the largest of the three species, and metamorphosis is completed within five days after fertilization without feeding. Thus, the development of *Astropecten scoparius* lies between *Astropecten aranciacus* and *Astropecten latespinosus*.

The development of sea-stars is generally divided into two types, one called the direct type and the other, the indirect type. The former is found in species having yolky ova and develops through brachiolaria only. Observations on the entire developmental process of the direct type have been carried out in more than ten species. On the other hand, little is known of the development and metamorphosis in species having indirect development, due mainly to the difficulties in rearing planktonic larvae for long enough to initiate metamorphosis. Thus, the entire process of indirect development has so far been reported only for a few species.

The distinction between the two types is, however, not given clearly, as pointed out by Chia (1968) and Komatsu (1975a), although the terms have been habitually used. Attempts have been made by some workers, therefore, to give precise definitions for the two types of development. Development without free larvae was called the direct type by Hyman (1955). However, the free swimming brachiolaria of *Crossaster papposus*, *Certonardoa semiregularis* or of *Asterina coronata japonica* may be called free larvae, although their development is definitely of the direct type (Gemmill, 1920; Hayashi and Komatsu, 1971; Komatsu, 1975b). Chia (1968) then gave a more precise definition, that development with a larva having a functional larval gut should be called the indirect type, and that without a functional gut, the direct type. This distinction could be a good cue for dividing all asteroid larvae into two groups. However, in practice, the terms, "direct" or "indirect" are too sweeping. It is doubtful whether the term "indirect type" can adequately be applied to the development of *Astropecten aranciacus* or *Astropecten scoparius*. This is because although the "indirect type" indicates that these animals have bipinnaria with functional gut, it fails to signify that they do not pass through the brachiolaria stage.

An alternative proposition is here presented for distinguishing the characteristic development from usual indirect type of development. Development having brachiolaria only, irrespective of whether it is pelagic or benthic, is called the direct type. Development which passes through both the bipinnaria and the brachiolaria is called the indirect type. With this distinction, all developments of asteroids may be divided into two groups except a few species, including *Astropecten* species. As described before, development of all astropectens so far known passes through only the bipinnaria, or its equivalent, and never through the brachiolaria stage. This may be an important feature of the development of this group and should not be overlooked. In this regard, the term "nonbrachiolarian type" is tentatively proposed for the developmental type exemplified by *Astropecten* species. The following shows a scheme proposed here:

Type	Bipinnaria	Brachiolaria
indirect type	+	+
direct type	−	+
nonbrachiolarian type	+	−

Besides *Astropecten* species, only members of the genus *Luidia* undergo metamorphosis without passing through the brachiolaria stage (Mortensen, 1913, 1938). No other asteroids have been known to take the nonbrachiolarian type of development here defined.

In association with the facts mentioned above, it may be worthwhile to focus on the aboral skeletal plate formation. Immediately after the completion of metamorphosis, the aboral skeletal system of *Astropecten scoparius* is composed of one central plate, one madreporic plate and ten plates which correspond to radial and interradial plates. The same composition was reported in *Astropecten aranciacus* and *Astropecten latespinosus* (Hörstadius, 1939; Komatsu, 1975a). However, the sea-stars of the majority of species immediately after metamorphosis do not bear a madreporic plate. Only a few species have been known to develop the madreporic plate, which is independent of the interradial plate, at the time of formation of the primary aboral plates. Among the former are *Asterina gibbosa, Asterias rubens, Leptasterias aequalis, Pentaceraster mammillatus, Certonardoa semiregularis* and *Asterina coronata japonica* (MacBride, 1896; Gemmill, 1914; Gordon, 1929; Mortensen, 1938; Hayashi and Komatsu, 1971; Komatsu 1975b). It was reported as a remarkable case that in *Leptasterias ochotensis similispinis* the madreporite appears as a rudiment at the second year after metamorphosis (Kano, Komatsu and Oguro, 1974). *Luidia savignyi* is the only species so far reported to have a madreporic plate at metamorphosis, besides the *Astropecten* species (Mortensen, 1938). A similar fact was observed in *Luidia quinaria* in this laboratory (unpublished data). It is of special interest that early formation of the madreporic plate seems to be associated with the nonbrachiolarian type of development.

The fact that the appearance of both remarkable features is confined to the genera *Astropecten* and *Luidia*, which are designated as typical representatives of primitive asteroids (Fell, 1963; Heddle, 1967), may indicate that some developmental features in asteroids are in fact related to the systematic position of the species.

The writers wish to express their cordial thanks to Dr. Katsuma Dan, Professor Emeritus of Tokyo Metropolitan University, and to Dr. Ryoji Hayashi, Professor Emeritus of Toyama University, for their valuable suggestions and critical reading of the manuscript. Their thanks are extended to Professor Kazuo Suzuki, Messers Hideki Yoshizawa and Shoji Akabane, Matsumoto Dental College, for scanning electron microscopy. They are also indebted to Mr. Akira Sakashita, Directer of Uozu Aquarium, for his kind cooperation, especially for aquarium facilities.

The present study was in part supported by a Grant-in-Aid to CO and MK (No. 054012) and a Grant-in-Aid to MK (No. 074102) both from the Ministry of Education of Japan.

Summary

1. *Astropecten scoparius* develops to a bipinnaria with simple ciliary bands and short bipinnaria arms through a wrinkled blastula by holoblastic, radial cleavage.

2. About seven days after insemination, the posterior portion of the bipinnaria becomes swollen and fine spicules appear on it, while the anterior portion, the stalk, remains unchanged.

3. Metamorphosis takes place gradually at the posterior portion, while the metamorphosing bipinnaria is pelagic. Two weeks after insemination, the stalk rapidly shrinks and the larva sinks to the bottom.

4. About 18 days after insemination, the juvenile completes metamorphosis with the opening of the mouth. The newly metamorphosed juvenile is 600 μ in diameter and each arm bears two pairs of the tube-feet, each having a sucker at the tip, and one terminal tentacle with red eye-spot.

5. The aboral skeletal system of the juvenile immediately after metamorphosis is composed of one central, one madreporic, ten radial and interradial plates, in addition to five terminal plates on the arms.

6. The juveniles smaller than about one cm in R do not bear some of the diagnostic features in this species.

7. A characteristic feature of the development of *Astropecten*, *i.e.*, the lack of a brachiolaria stage, is stressed. The term "nonbrachiolarian type" is tentatively proposed to distinguish the development of *Astropecten* and *Luidia*, which do not pass through a brachiolaria stage, from the usual indirect type of development.

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